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CONDITIONS GOVERNING THE EVOLUTION AND DISTRIBUTION OF TERTIARY FAUNAS

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The subject allotted me being "The Conditions Governing the Evolution and Distribution of Tertiary Faunas," I may begin by stating certain propositions which, for the purposes of this discourse, may be assumed as axiomatic.

1. A fauna is an assemblage of organic species populating a given area at one and the same epoch, and—allowances being made for the preferences of such minor groups as carnivorous, phytophagous, littoral, benthal, petricoline, and limicoline animals—having for the most part identical geographical distribution.

2. We may regard it as indisputable that the properties of the environment shown to influence a living fauna, or to control its distribution, were capable in Tertiary[2] times of exerting an analogous influence on faunas now known chiefly by their fossil remains; and, conversely, if in a fossil fauna we are able to trace certain definite features, which in a living assembly would result from a particular environment, we are justified in concluding that the fossil fauna in

[1] Dr. F. H. Knowlton's article on "Succession and Range of Mesozoic and Tertiary Floras," which should have appeared as No. X in this series, has never reached the *Journal of Geology* and does not appear, therefore in its proper place. Should the article be submitted later, it will be published.

[2] The author realizes that these factors may not be entirely applicable to the faunas of pre-Tertiary epochs.

question was, when living, subject to the action of an analogous environment.

To illustrate this second proposition it may be said that if fig trees can now flourish and reproduce their species only in regions having a mean minimum temperature of thirty degrees Fahrenheit, and a summer mean temperature of not less than sixty degrees; and, secondly, if we find in the Tertiary leaf-beds of Greenland and Spitsbergen indications of groves of fig trees having flourished there in the Oligocene epoch; then we are likewise justified in assuming that in Greenland at that epoch the summer mean temperature did not fall far below sixty degrees, nor the winter cold maintain itself greatly below the minimum above mentioned.

Among marine animals a consensus of the evidence on record points insistently to temperature as the most important factor in determining the existence and persistence of species in a given area; and the toleration oi an organism and its progeny for fluctuations of temperature limits its geographical distribution as positively as would a material barrier. In the absence of such mortal extremes of temperature, material barriers, unless hermetically complete, really count for very little in determining distribution.

In utilizing fossil faunas as chronologic indicators of geologic time, the marine faunas are more readily utilized for the grand divisions of the scale than the land faunas, especially when the latter are characterized chiefly by fossil vertebrates. This is because the marine conditions are more uniform, less affected by meteorologic factors, and more dependent upon conditions which affect the whole hydrosphere rather than small areas of it. The struggle for life is less intense, the food supply generally more adequate, enemies less vigorous, and dangerous fluctuations of temperature far less frequent, in the sea than on land.

The same features make the land faunas more clearly indicative of minor divisions of the scale, and of the progress of organic evolution in the general region concerned; while less conclusive as to the contemporaneity of widely separated though analogous faunas.

The liability to sudden extermination by epidemic diseases, or by sharp meteorologic changes of very short duration, or even by the incursion of multitudes of small enemies, insects, or carnivora injuri-

ous to the young, is vastly greater among the land vertebrates than among marine animals. Marine vertebrates are more subject to injury from temporary causes than are the invertebrates associated with them. A marked instance of this was the destruction of the "tilefish" of the middle Atlantic coast a quarter of a century ago, if the explanation finally accepted as most probable by Professor Baird and other experts be the true one. The "tilefish" inhabited a region where the water, warmed by the proximity of the Gulf Stream, was of a moderate temperature. The combination of violent winds from a quarter which led to the forcing to the eastward of the Gulf Stream water, and to the influx of much colder water from the Polar current into the area thus vacated, was believed to be responsible for the almost total extermination of these fishes, which were found floating dead and apparently uninjured in millions on the surface of the sea, by navigators bound into New York and adjacent ports.

This temperature change which lasted at most for a few weeks would probably have had no effect whatever on the adult larger invertebrates of the same area, though to any of their larval young it might well have proved fatal. Another season would replace these, but the restocking of the fauna with "tilefish," which finally took place, required many years.

A statement of the factors which are regarded as modifying existing marine invertebrate faunas will put the student in possession of the chief factors which may have affected analogous faunas during past geologic time. My point of view is that afforded by a knowledge of conditions affecting molluscan life.

Census of species.—From a discussion too long to quote here in full,[1] I have drawn the following conclusions: That the part of the average mollusk-fauna which is capable of leaving traces in the shape of fossils, under conditions not greatly differing from those of the present day, in a region where the temperature of the sea ranges during the coldest winter month between 32° and 40° F. (which might be called *boreal*), would comprise about 250 species. In case the temperature ranged between 40° and 60° (*cool temperate*) about

[1] *Bull. U. S. Geological Survey, No. 84,* Correlation Papers, Neocene, 1892, pp. 25–28.

400 species might be expected. With a range between 60° and 70° (*warm temperate*) we should find about 500 species, and in the *tropical* zone (70° to 80° F.) not less than 600 species; and in specially favorable localities of the tropics nearly twice as many.

Learning from the characteristic genera what zone of temperature a given fauna may have belonged to, we can with confidence predict approximately the number of species which it will prove to contain when fully explored. Of course in a single locality where the characteristic situs is exclusively mud, or rock, or fine sand, only a certain proportion of the total fauna will be represented, but these minor groups are not entitled to the designation of a fauna as used in this paper.

Relations of temperature to the fauna.—In considering the relations of temperature of the water to the fauna, account must be taken of the vertical differences. The temperature of the water at the surface differs materially from that at the bottom in most regions, where the depth is over a few fathoms. Arctic or Antarctic species may extend in cold depths of ocean for thousands of miles; while, in the warm superficial strata above them and inshore from them, a totally different assembly lives and thrives. It is easy, in the case of widely diffused northern species, when deep water dredgings have revealed the distribution, to observe in the tables the boreal forms descending with the temperatures to deeper and deeper water as they approach the tropics. That this is so generally true is satisfactory evidence that the factor of pressure, being equalized by thorough permeation of the organism, is less effective in limiting distribution than most other factors. It seems incredible that the large eggs of abyssal mollusks can go through the processes of development under a pressure of tons to the square inch; since there must be a limit somewhere to the permeability of tissues. Still it is evident that they do.

Why temperature should be so important in limiting distribution is a question which may be answered in several ways. Brooks has shown that, while the embryonic oysters (*Ostrea virginica*) are swimming at the surface of the sea, an entire brood may be destroyed to the last individual, by a fall in temperature of a few degrees, due to a cold rain. While it is not improbable that oysters from the northern part of the range of the species, say Nova Scotia, may have in the embry-

onic state a greater tolerance for a fall in temperature than those of a relatively warmer region like Chesapeake Bay or the coast of Florida, yet it seems likely that a certain narrow range of temperature is required for the developmental stages, and that the distribution of the species is limited to the area where such temperatures may be had during the spawning season.

Thus, for example, young Chesapeake oysters of an inch and a half in breadth may be transported to the Pacific coast, planted in suitable locations, and will flourish well, growing even faster than in their native waters. Yet of the billions of spat which these oysters have discharged into the waters of the Pacific (fifteen or twenty degrees colder than the Chesapeake at spawning time) there is not a trace left in the shape of young oysters. In spite of the best efforts of the local oystermen the Chesapeake oyster has not become acclimated.

Another way in which temperature may affect a fauna is in promoting or inhibiting the minute plant-life which forms the food of many bivalves. In all cases it is certain that a fall below a certain level of temperature is more effective upon the animals subjected to it than a corresponding rise in temperature. The first, as I have indicated, may kill; the second, merely accelerate development.

The very low temperatures nearly universal on the floor of the open ocean, and the otherwise uniform conditions that prevail there, offer favorable opportunities for wide distribution of boreal organisms. I am informed by Mr. A. H. Clark that the Antarctic Crinoidea, characterized by scaly segments, have penetrated by this road in the Eastern Pacific even to the Oregonian region; while on the opposite coast the smooth-segmented Arctic forms have been traced far to the southward.

As indicators of subaerial conditions it is obvious that littoral invertebrates are more useful than those of deeper waters, since they are more exposed to climatic changes. It may happen that a vertical section of the submarine continental slope drawn at right angles to the coast from the shore to the oceanic floor may, and in most cases will, cut through a series of different faunas corresponding to the temperatures encountered. Off Cape Hatteras the cold inshore current from the north is the haunt of a cool-temperate fauna with

some boreal elements. Thirty miles off shore, in less than fifty fathoms, the fringe of the Gulf Stream protects a fauna in large part identical with that which characterizes the Bahama Banks and Bermuda. The large species of Venus, which penetrated to the north shore of the Gulf of Mexico with the cool Miocene water, have maintained themselves notwithstanding the subsequent rise of temperature and persist in these new conditions to the present day, a notable example of adaptation. On the other hand the subtropical Rangia and Corbicula, which advanced with the warm Pliocene waters far to the north of their original station, have left only sparsely scattered fossils as an indication of their invasion.

In the later Tertiaries the proportion of recent species is sufficient, taking into account the present distribution of these species, to afford the means for a very probable estimate of the temperature which prevailed during the particular portion of Tertiary time when they formed part of the fauna. An interesting example of this is afforded by a small collection of fossils obtained by Stimpson in 1865, from above the lignitic coal measures in the northeast angle of the Okhotsk Sea, in Penjinsk Gulf.[1] I have reported in full upon these fossils, and it is sufficient to say on this occasion that the climate and recent fauna of the locality are Arctic and the open water of the sea persists only for some three months of the year, while the species of fossils indicate that during their existence in the living state the annual mean air temperature, at the most moderate estimate, must have been 30° to 40° F. warmer than at present. Another instance has recently been brought to my attention. During the two seasons just past, collections have been made from the Pliocene auriferous gravels of the coast of Alaska near the town of Nome.[2] Thirty-three species have been identified of which seven appear to be new, eleven are now known living only south of the line of floating ice in winter, one is a Miocene species, and the remaining fourteen are common to the Alaskan fauna in general from the Arctic to British Columbia. This

[1] *Proc. U. S. Nat. Mus.*, Vol. XVI, No. 946, 1893, pp. 471–78, pl. LVI. The age of the fossil shells in the report upon these fossils was given as Miocene, but it is probable that like the analogous lignite deposits of the adjacent shores of America, the underlying coal measures may be referable to the Upper Eocene or Oligocene and may have been laid down contemporaneously with the American Kenai formation.

[2] Cf. *Am. Jour. Science*, Vol. XXIII, June, 1907, pp. 457, 458.

indicates clearly that during the Pliocene, when these gravels were being laid down, the climate of Norton Sound, now subarctic, was not colder than that of North Japan or the Aleutian Islands where the sea remains unfrozen throughout the entire year. This agrees well with the evidence from the marine Pliocene of the northeastern corner of Iceland, which has afforded over one hundred species, of which seventy-four are said to be common to the Crag fauna of the British Islands, corresponding to an annual mean air temperature not lower than 42° F., while it is hardly necessary to say that the present conditions in north Iceland are purely Arctic. A little patch of Pliocene at Gay Head, Mass., afforded a fragment of the genus Corbicula, now warm temperate in its distribution; while the older of the deposits at Sankoty Head, Nantucket, as well as those at Nome, show that some of the species which ranged at that period from Bering Sea to the North Atlantic are now strictly confined to temperate waters in their respective hemispheres.

I have given most of my time to the relations of temperature to faunas, as this is the most important, pervasive, and obvious factor of the modifying environment, but there are a few others which may be briefly alluded to.

The question of food is next in importance to temperature. It is true that the ocean almost everywhere is a generous provider for its inhabitants, so that only special scrutiny reveals important differences in the food supply, a large part of which is furnished by almost microscopic animals. Yet it has been conclusively shown that in places where a persistent movement brings constantly fresh supplies of food and well-aerated water, as on the continental slope washed by the Gulf Stream, or where the periodical ebb and flow of the tides do the same thing on a smaller scale—there the oceanic population flourishes with especial vigor and abundance. Near the shores a special quota of plant-feeders live, in their turn furnishing provender for carnivorous species. The distribution of plant food in the shape of algae thus governs the distribution of the phytophagous species. We find on the basalts, andesites, and recent lavas of the Aleutian chain of islands, enormous groves of kelp and meadows of olivaceous rock-weed. Whether because of something in the chemical composition of these rocks, or otherwise, the red and green seaweeds are

almost wholly absent from them. However, where the granitic masses which form the core of some of the islands (and in other places stand alone, domelike in the sea) are within reach of the waves, we find a special flora of the more bright-colored algae and a special fauna dependent upon them. No matter how isolated the patch of granite, the characteristic animals recur, and in many cases reproduce in their own tints the rosy hue of the plants upon which they depend for food.

In the abysses where the absence of sunlight excludes plant life the animals are almost exclusively carnivorous and largely subsist on the abundant rain of dead organisms which slowly descends from the surface layers of the sea.

It has been customary to regard the 100-fathom line as constituting a sort of boundary between the fauna of the shores and of the deeps. This has a certain foundation in the fact that at greater depths no living algae can exist for want of sunlight. A more or less constant migration, casual or accidental, is constantly taking place between the littoral region and the deeps, but it is so slow, and the process of adaptation to the new conditions so gradual, that we may safely regard the abyssal fauna as even geologically old. I have called attention to certain features of the eastern Pacific and Antillean abyssal faunas which illustrate these remarks in the introduction to a recent monograph.[1]

Freshwater and terrestrial invertebrates are subject not infrequently to one set of influences which is rarely noticed in the open sea. This is, in the case of the limnophilous species, a change in the mineral content of the water in which they live. This is usually gradual and when injurious chiefly due to the concentration of salts (which exist in all freshwaters arising from drainage) by evaporation. In the case of many large Pleistocene lakes, of which the prehistoric Lake Bonneville may be taken as an example, this process has been carried on until the saline content of the water became so excessive that all molluscan life became extinct, as in the Great Salt Lake of Utah. A careful study of the beds of shell-marl deposited by the shrinking lake shows that the effect of the gradually increasing salinity of the water on the freshwater mollusks contained in it was

1 *Bull. Mus. Comp. Zoölogy*, Vol. XLIII, No. 6, October, 1908, pp. 205–12.

to lead to a thickening and corrugation of the shell, a tendency to longitudinal ribbing, and a diminution in average size, all of which changes may perhaps be due directly to the astringent action of the salts of sodium and magnesium upon the thin and delicate margin of the mantle which secretes the additions to the shell. These characteristics become more and more pronounced as the waters become more saline, until finally the conditions become too rigorous for survival. The gradually intensified effect of the increase of salinity may be beautifully illustrated by a collection of the fossil shells from the successive marl beds around Great Salt Lake. Another instance, probably of the same nature, is afforded by the marls of Steinheim, in Wurtemburg, of which the mutations shown by the species of Planorbis, in particular, are described in the well-known monograph by Hyatt.[1]

A somewhat similar effect seems to be produced in the case of landshells inhabiting arid volcanic islands in windy regions. Here the astringent effect appears to be produced by the alkaline volcanic dust to which these animals living on almost bare shrubs or among sparse herbage are more or less constantly exposed. I have called attention to the conditions under which this effect seems to be produced in a paper on the landshell fauna of the Galapagos Islands.[2] This illustrates how upon animals of quite different systematic relations, similar effects, simulating an apparent convergence, may be caused by the direct action of the environment upon individuals. Paleontologically these instances are worth noting, as otherwise the forms concerned might well be regarded as belonging to totally different groups from the individuals which developed normally in an ordinary habitat.

In conclusion I may call attention to certain factors which have serious importance in modifying the fauna of a large extent of coast catastrophically, and which inferentially are to some extent responsible for the marked changes we observe in different stratigraphic horizons where we do not find indications of coincident orogenic changes.

[1] "Genesis of the Tertiary Species of Planorbis at Steinheim," *Anniv. Mem. Boston Soc. Nat. History*, 1880, pp. 114, pls. I–IX, 4to.

[2] "Insular Landshell Faunas, Especially as Illustrated by the collection of Dr. G. Baur on the Galapagos Islands," *Proc. Acad. Nat. Sciences, Philadelphia*, August, 1896, pp. 395–459.

In some regions, as the west coast of the Floridian peninsula, the strata may be slightly inclined so that the beds between which subterranean waters move have their edges beneath the sea. Torrential rains in the interior of the peninsula carry vegetable matter into the interstices of the soft limestone rocks, where it decays with the accompanying production of carbon dioxide and sulphuretted hydrogen gas. This accumulates and under the hydrostatic pressure of an exceptionally heavy rainfall is sometimes forced out beneath the sea from the edges of the submerged strata in sufficient volume to kill by suffocation every living thing along many miles of coast. This has happened on the coast of Florida several times within my recollection. The repopulation of the devastated area is slow and can rarely reproduce exactly the same assemblage of animals which previously occupied that area.

Another mode in which widespread extermination of a sedentary population of invertebrates may be brought about is by the sudden appearance of vast multitudes of minute organisms like *Peredinia*. Within the last few years, both on the coasts of Japan and of California, the sea at times has been covered for miles with reddish clouds of these submicroscopic creatures. On their advent near the shore, driven by wind or currents, the shellfish, corals, and fishes are rapidly suffocated, and, if the pest continues, everything within the area it occupies will succumb. I have heard that, within two years, the Japanese pearlshell preserves on the seashore of that country have been almost wholly ruined by the organisms referred to, with the loss of hundreds of thousands of dollars, to say nothing of years of labor rendered fruitless.